OPTIMAL NICHE SPACE OF THE RED-WINGED BLACKBIRD. III. GROWTH RATE AND FOOD OF NESTLINGS IN MARSH AND UPLAND HABITAT

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Red-winged Blackbirds (*Agelaius phoeniceus*) nesting in marshes generally have higher reproductive success than those nesting in uplands (Case and Hewitt, 1963; Robertson, 1972). Marsh habitats and their associated ecological features therefore represent a more nearly optimal part of the fundamental niche of the Redwing than do upland habitats. The difference in survival value between the two habitats is largely due to differences in the proportion of nests destroyed by predators. However, the relative abundance of food for nestlings might also be expected to play an important role in determining the survival value of a nesting habitat. Marshes are usually more productive than upland habitats and have a food source, in the form of emergent aquatic insects, that is rapidly and continually renewed (Orians, 1969). The purpose of this paper is to examine the role of food supply in determining the survival value of a nesting habitat by comparing the types and source of food brought to nestlings, the growth rate of nestlings, and the incidence of starvation in nestling populations of Redwings in marsh and upland habitats.

NESTLING FOOD HABITS

The food brought to nestlings is usually 100 percent animal matter, with a preponderance of insects and occasional arachnids, mollusks, and miscellaneous items (Allen, 1914; Neff and Meanley, 1957; Bird and Smith, 1964; Snelling, 1968; Orians and Horn, 1969; Voigts, 1970). In most cases, only the female feeds the nestlings, but occasionally a male assists (Orians, 1961*b*; Case and Hewitt, 1963). After the young have fledged, the male regularly feeds them (Beer and Tibbits, 1950; Orians, 1961*b*). Some of the food for nestlings is obtained in the vicinity of the nest, but much food is gathered from areas outside the male's territory (Beecher, 1942) and in many cases outside the nesting habitat at some distance from the nest (Orians, 1961*a*; Case and Hewitt, 1963; Wiens, 1965; Snelling, 1968).

METHODS

Two marsh colonies and three upland colonies of Redwings were studied during the breeding seasons of 1968, 1969, and 1970. All of the study areas are within a 25 mile radius of New Haven, Connecticut.

Both marsh habitats are freshwater cattail marshes bordered on at least two sides by large stands of deciduous woodland and in close proximity to pasture or early stages of old field succession. Clarkes Pond is an impoundment on the Mill River that covers an area of 4.65 ha; 1.92 ha is occupied by cattails (*Typha latifolia* and *T. angustifolia*) and the remaining 2.73 ha is open water with some pondlily (*Nymphaea* sp.), pickerelweed (*Pontederia* sp.), and arrowhead (*Sagittaria* sp.). The flow of the Mill River keeps the water at a fairly constant level year-round. All Saints Marsh covers an area of 1.09 ha, all of which is occupied by a moderately dense stand of *Typha latifolia* interspersed with small patches of open water. Buttonbush (*Cephalanthus occidentalis*) forms a dense tangle in some areas. This marsh has no flowing inlet, but in spring and early summer there is a trickling outflow, apparently fed by springs in the marsh. In some years the marsh dried up in late summer. This may account for an apparently low abundance of emergent aquatic insects in this marsh compared with Clarkes Pond.

The upland sites all consist of rather poor quality hayfields supporting a mixture of timothy (*Phleum pratense*), bromegrass (*Bromus* sp.), orchard grass (*Dactylis glomerata*), red clover (*Trifolium pratense*) and alfalfa (*Medicago sativa*). Sturdy "weed" species such as dock (*Rumex* sp.) are quite abundant and frequently were used as nest support. Hyland Farm (2.68 ha) and Augur Jr. (9.85 ha) are bordered on at least two sides by stands of deciduous woodlands and hedgerows. Lyman Golf (2.99 ha) is bordered by hayfields and is located about 200 m from a large stand of mixed deciduous trees bordering a small stream. More complete habitat descriptions are recorded in Robertson (1972).

Throughout the nesting season, except during periods of rainy weather, each colony was visited once every three days. Nests were usually located during construction or egg laying and marked with a numbered bamboo pole. Individual recognition of nestlings was achieved by marking combinations of anterior or posterior, right or left tarsi with water-proof ink from a felt-tipped marking pen. Weights, to the nearest gram, were measured by placing the nestling in a plastic cup and weighing with a 100 g capacity Pesola spring balance. Tarso-metatarsus length to the nearest 0.1 mm was measured with vernier calipers using the method described by Kalma (1970).

Samples of the types of food brought to nestlings were obtained using the pipe-cleaner neck collar technique (Willson, 1966). Collars were placed on all nestlings in a nest for a period of 30 to 60 minutes, during which the female delivered food. The unswallowed food was then removed from the throat of the nestlings, stored in 70 percent alcohol for later identification, and the collar removed. A given brood was sampled no more than once every three days. The effect of food deprivation for one hour every third day on nestling growth was considered negligible. Many nests were never sampled and many were sampled only once. A total of 169 brood samplings were made and food was obtained in samples from 110 nests. Some females reacted negatively to the collars and tried to remove them rather than feeding the nestlings. In some cases, when food was not swallowed, the female would remove it and, if no nestling would swallow it, eat it herself. This technique is not reliable, therefore, as an absolute measure of feeding rates. However, it is assumed that the food items obtained in the samples are representative of the type of food brought to the nestlings, so the technique is very useful for comparative purposes (cf. Orians, 1966; Orians and Horn, 1969). Food sampling was done throughout the nesting season and at times ranging from early morning to evening. Observations from portable blinds were made to determine the habitat origin of food items brought to nestlings.

In 1969 and 1970, several clutch and brood size manipulations were made to determine whether birds in one habitat were more closely faced by food limitation than the other. It was expected that females would be most capable of raising artificially enlarged

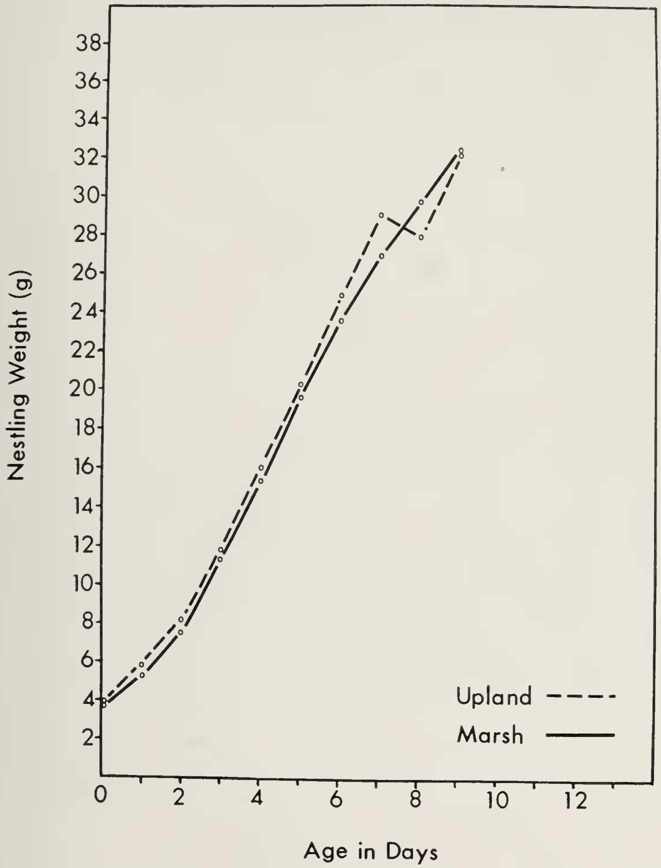

FIG. 1. Growth of Redwing nestlings shown by mean daily weights. Growth curves are composites including nestlings of both sexes for all years of the study.

broods in the habitat that had the highest relative abundance of food. Transfers of eggs or nestlings were made only between nests known to be of exactly the same stage in the nesting sequence.

RESULTS

Growth Rate.—The mean weight of nestlings at 9 days of age, the last day before fledging when most nestlings were still available for weighing, was 32.39 ± 0.34 g (± 1 SE) for nestlings from marshes and 32.19 ± 0.86 g for those from uplands. This similarity in mean weight at fledging suggests the growth rate of nestlings in the two habitats is the same. The composite growth curves for all years of the study and for all nestlings of both sexes from marshes and uplands (Fig. 1) show the form of the curve for the first

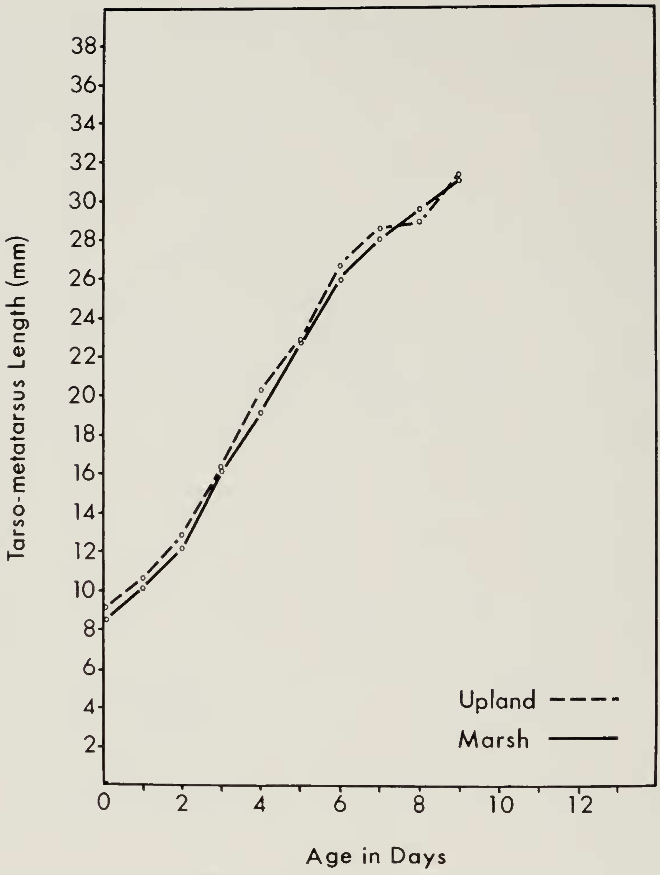

FIG. 2. Growth of Redwing nestlings in 1970 as shown by mean daily tarso-metatarsus lengths (male and female combined).

7 days is similar. The growth rates, as measured by the length of the tarso-metatarsus, gives the same result (Fig. 2). Mean weight and mean tarso-metatarsus length are not significantly different for marsh and upland nestlings at age 9 days. A decrease in mean weight of upland nestlings from day 7 to day 8, and a period of slow tarso-metatarsus growth from day 7 to day 8, result in the upland nestlings, which were previously slightly larger, fledging at about the same weight and tarso-metatarsus length as marsh nestlings. Growth curves for 1969 and for 1970 analyzed separately have the same form as the combined curve for both years, with the mean daily weight of upland nestlings consistently greater than for marsh nestlings until day 8. In both years, upland nestlings show a decrease in mean weight

TABLE 1

REDWING PRODUCTIVITY IN MARSH AND UPLAND

	Marsh		Upland
Nests			
No. Full Clutches	654		145
Mean Clutch Size	3.50 ± .02	*	3.37 ± .06
Fledged/Successful Nest	2.71 ± .05	ns	2.49 ± .13
Area			
No. Active Nests/ha-yr.	100.5		7.7
Fledged/ha-yr.	132.7		5.4

* $P < 0.05$; ns = not significant.

from day 7 to day 8, resulting in their weight near fledging on day 9 being the same as for marsh nestlings.

To compare the rate of nestling growth in different parts of the nesting season, the season was divided into early, middle, and late portions. The middle, or peak, portion of the nesting season was designated as the smallest number of consecutive days required to include 50 percent of the active nests, dated by day of clutch completions, in each colony. Early and late portions include nests with clutch completion before and after the peak

TABLE 2

FREQUENCY DISTRIBUTION AND SUCCESS OF VARIOUS CLUTCH SIZES IN MARSH AND UPLAND. MANIPULATED CLUTCHES ARE NOT INCLUDED

	Clutch Size				
	1	2	3	4	5
Percent (No.)					
Marsh	0.3(2)	4.7(28)	43.0(254)	50.0(295)	2.0(12)
Upland	0.7(1)	10.1(14)	43.5(50)	43.5(60)	2.2(3)
Percent Successful					
Marsh	100.0	50.0	59.8	61.7	41.7
Upland	0.0	57.1	31.7	43.3	33.3
Fledged/Successful Nest					
Marsh	1.00	1.64	2.33	3.09	3.80
Upland	0.00	1.38	2.11	3.08	4.00
Fledged/Egg					
Marsh	1.00	0.41	0.46	0.48	0.32
Upland	0.00	0.39	0.22	0.33	0.27

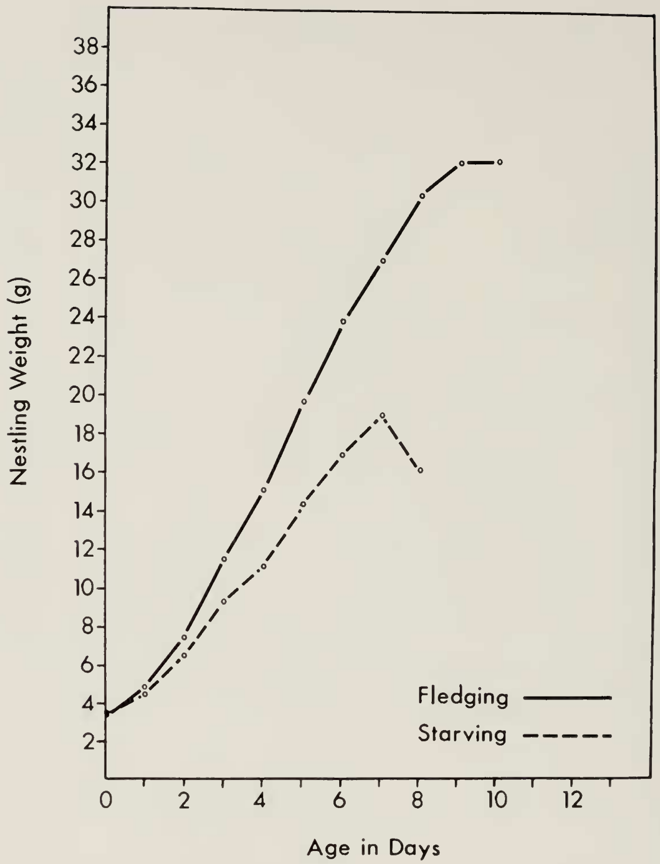

FIG. 3. Comparison of growth (mean daily weight) of nestlings that eventually fledge and those that die of starvation for all marsh nestlings in 1970.

respectively. Separate analyses indicated that within habitat types there were no significant differences in over-all growth rates, nor in growth rates of nestlings of a given brood size, for nestlings hatched in different parts of the season. Also, within a given habitat, there were no consistent or significant differences in growth rate or mean weight at fledging between individuals in different sized broods.

Redwing Productivity.—The initial productivity of individual Redwing females, as measured by clutch size, is on the average significantly ($P < 0.05$) greater in marsh than upland habitats (Table 1). The larger mean clutch size in marshes results from a frequency distribution in which four is the most common clutch size (Table 2). In uplands, clutches of three and four are equally common and clutches of two are more common than in marshes. Ignoring the clutches of one because of small sample size, the most common clutch size in marshes (four) is also most successful both in the proportion of nests that fledge at least one young and the number fledged per egg laid. However, for those nests that fledged at least one nestling, clutches of five are more productive than clutches of four; the mean number of young fledged per successful nest is directly related to clutch size.

The larger mean clutch size of marsh nesting Redwings may make some contribution to the productivity as measured by mean number of young fledged per successful nest (Table 1). Although this figure is not different statistically between the two habitats, because of higher variability and smaller sample size of fledging nests than clutch sizes, marsh nests tend to have a larger number fledged per successful nest than those in uplands.

The combination of greater nesting density and larger number of young fledged per active nest results in productivity measured by the number of young Redwings fledged per hectare being much greater in marshes than in upland habitats (Table 1).

Starvation.—Mortality of a small and nearly equal portion of nestlings in both marsh and upland habitats was attributed to starvation or a starvation-diarrhea syndrome. The nestlings dying from starvation showed a lower rate of growth than those that eventually fledged (Fig. 3). Many of them also failed to form fecal sacs and as a result the nest became fouled (see also Haigh, 1968). This sometimes led to a deterioration of condition of the entire brood. Bacterial-culture analyses from gastrointestinal tracts of nestlings that failed to form fecal sacs were done at the University of Connecticut Department of Animal Pathology. These tests provided no evidence of pathogens responsible for the diarrhea aspects of this syndrome (S. Wyant, pers. comm.), but this possibility cannot be ruled out. However, since this condition was often preceded by poor weight gain, nestlings in this condition were combined with those dying of starvation per se into a starvation-diarrhea syndrome category, subsequently referred to as "starvation."

Starvation occurred in 18.8 percent of the broods in marshes and in 17.2 percent of those in uplands (cf. Table 3), and 10.8 percent of the marsh nestlings and 7.5 percent of the upland nestlings died of starvation (cf. Robertson, 1972). Neither of these proportions are significantly different between habitats. Comparisons of the proportion of broods having some starvation also reveal no differences between habitat for each brood size, and no statistically significant differences within habitat between broods of one, two, three, four, and five (data are recorded in Robertson, 1971). Broods of six, which have not been found to occur naturally in Connecticut, were

TABLE 3

PERCENTAGE OF BROODS WITH SOME NESTLINGS STARVING AS A FUNCTION OF TIME OF EGG-LAYING

See text for explanation of categories. The total number of broods in each category is in parentheses.

Site	Early	Peak		Late	Total
	Percent Broods with Some Starvation				
Marsh #					
CP '68	0 (18)	3.5(57)		4.0(25)	3.0(100)
CP '69	0 (12)	2.9(69)	**	43.7(48)	17.8(129)
CP '70	0 (14)	0 (46)	**	24.4(41)	9.9(101)
AS '69	5.9(17)	23.2(56)	**	76.5(17)	30.0(90)
AS '70	0 (14)	*35.9(53)		51.7(29)	35.4(96)
Total					18.8(516)
Upland					
HF '69	0 (1)	11.1(9)		25.0(12)	18.2(22)
HF '70	0 (0)	0 (6)		25.0(4)	10.0(10)
AJ '70	0 (8)	18.2(11)		0 (6)	8.0(25)
LG '70	12.5(8)	50.0(14)		0 (2)	33.3(24)
Total					17.2(99)+

* $P < 0.05$, ** $P < 0.01$ that difference between adjacent categories is due to chance. + Total includes 18 nests from other upland sites, # CP = Clarkes Pond, AS = All Saints Marsh, HF = Hyland Farm, AJ = Augur Jr., LG = Lyman Golf, '68 = 1968, '69 = 1969, '70 = 1970.

obtained by clutch or brood size manipulations. In marshes, a significantly higher proportion of broods of six had some mortality by starvation than the smaller brood sizes.

Although the rate of growth and size of nestlings at fledging is the same in different parts of the nesting season, the incidence of starvation increases throughout the season (Table 3). All nine colonies studied showed a trend of a larger proportion of nests with starvation during the peak of activity than before, and seven of nine colonies had a larger proportion of nests with starvation after the peak than during the peak of activity.

Type and Source of Food.—The proportionate distribution of food types by sample and by food item in the diet of nestling Redwings in marsh and upland habitats is shown in Table 4. Lepidopteran larvae were found in about the same proportion of samples from the two habitats, but they comprised a greater fraction of the individual food items brought to marsh than to upland nestlings. A smaller fraction of the marsh samples contained

TABLE 4

PROPORTIONATE DISTRIBUTION OF FOOD TYPES BY SAMPLE AND FOOD ITEM IN THE DIET OF NESTLING REDWINGS IN TWO HABITATS

A sample includes the food delivered to all individuals in a brood during a sampling period.

	Samples		Items	
	Marsh	Upland	Marsh	Upland
Number	89	21	500	135
Percentage with Terrestrial food source				
Lepidopteran larvae	74	71	42	26
Misc. terrestrial	29	71	13	72
Total	–	–	55	98
Aquatic food source				
Odonata	37	5	21	1
Misc. aquatic	31	0	12	0
Total	–	–	33	1
Unidentified food source				
Misc.	40	5	12	1

All pairwise proportionate differences are significant ($P < 0.01$) determined by χ^2, except samples of lepidopteran larvae.

miscellaneous items such as arachnids, spittle insects, and beetles that were known to have a terrestrial origin; these items made up a significantly smaller portion of the marsh nestling's diet. Conversely, a larger proportion of marsh than upland samples contained odonates and other food items of aquatic origin, as well as items of uncertain habitat origin, and these items also comprised a significantly larger portion of the diet of marsh nestlings. Many single samples from marsh nests contained both items from aquatic and terrestrial habitats. At least 55 percent of the items in the diet of marsh nestlings were obtained from terrestrial habitats and 33 percent were from aquatic habitats. Ninety-eight percent of the food items in the upland nestling's diet were from terrestrial habitats.

There were also differences in the proportionate distribution of nestling food items between individual marshes. Lepidopteran larvae comprised a significantly ($P < 0.01$) larger proportion of individual food items brought to nestlings in All Saints Marsh (57 percent) compared with Clarkes Pond (34 percent) and odonates comprised a larger proportion ($P < 0.01$) in Clarkes Pond (31 percent) compared with All Saints Marsh (1 percent). No differences in proportionate distribution of food items occurred between upland habitats.

DISCUSSION

The growth rates of nestlings in marshes and uplands are similar in that they result in the same average weight at fledging for nestlings in both habitats. This suggests that the relative abundance of food is roughly equal for females nesting in marshes and uplands. Holcomb and Twiest (1970) also reported that there was no difference in growth of Redwings raised in either marsh or upland habitat, but they noted some brood reduction in uplands that was apparently attributed to starvation (cf. Parker, 1968). Although there was no differential starvation or brood reduction between habitats in this study, there was an increase in the occurrence of starvation late in the season (cf. Table 3) while the growth rate showed no seasonal trends. Rate of growth, and mean weight at fledging, when used alone, are therefore not necessarily good indicators of the availability of food for nestlings. A difference between habitats in the proportion of broods with some nestlings starving is a better indicator of the relative abundance of food.

Measured by either index, the relative abundance of food was apparently equal for nestlings in marsh and upland habitats. The fact that there was no differential starvation between habitats in broods of a given size, especially large broods, is also indicative of similarity in relative abundance of food.

Within a given habitat, the growth rate and incidence of starvation were the same for broods of different size (cf. Royama, 1966; Ricklefs, 1968). Brenner (1964) made similar observations and also noted a constancy of growth rate throughout the season. This relationship, and the fact that, compared with smaller broods, a significantly larger ($P < 0.01$) proportion of the artificially enlarged broods of six had some nestlings starve, suggest the brood size of females is adapted to the number of offspring that the parents can nourish (Lack, 1954).

Starvation resulted in the mortality of about 10 percent of the nestlings in both marsh and upland habitats. Predation accounted for a greater proportion of mortality in both habitats, but especially in uplands where 34 percent of the nestlings were taken by predators (Robertson, 1972). In a study of Redwings nesting in marshes in Illinois, starvation accounted for the mortality of less than 1 percent of the nestlings (Smith, 1943). In Wisconsin, Young (1963) recognized no starvation; however, some of the mortality where nestlings were found dead in the nest (5.2 percent) or had disappeared (24.1 percent) may have been due to starvation (Haigh, 1968). During a three-year study in eastern Washington, Haigh (1968) found that between 40.7 percent and 58.6 percent of the nestlings died of starvation, the most common single cause of nestling mortality.

The difference in the incidence of starvation between marsh habitats in eastern Washington and habitats in Illinois or Connecticut may be ultimately due to competitive interactions between Redwings and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) in western North America where the two species are sympatric. Marshes in general are more productive in the arid and semiarid regions of the West than in the humid regions of central and eastern North America (Orians and Horn, 1969), and the geographic range of the Yellowhead is limited to those regions where the productivity of lakes and marshes is high (Willson and Orians, 1963). In the zone of sympatry, Redwings are excluded by Yellowheads from the most productive marshes, or at least are forced to nest near wooded shores (Willson and Orians, 1963; Orians, 1966; Miller, 1968). Therefore, Redwings are not able to take advantage of the food supply of the most productive western marshes and must rely on upland habitats as a source of a large portion of their food (Orians and Horn, 1969). Since the upland foraging areas in the West are probably not as productive as the eastern deciduous forests, where Redwings obtain large numbers of lepidopteran larvae, the relative availability of food is perhaps lower, and the incidence of starvation higher, in the arid regions of the Redwings' geographic range.

In both marshes and uplands, female Redwings spend a large portion of their foraging time in mixed deciduous woodlands that border the nesting habitat. Observations revealed these woodlands to be the source of lepidopteran larvae that occurred in over 70 percent of the food samples from nests in either habitat. Wiens (1965) found that Redwings nesting on Lake Wingra in Wisconsin obtained the bulk of their food (lepidopteran larvae) in the hardwood forests bordering the marsh, and Snelling (1968), on the same marsh, reported that female Redwings spent 16 percent of their time foraging on the marsh and 45 percent of their time off the marsh, presumably foraging a large portion of this time. This would suggest that marsh-nesting Redwings have little advantage over upland birds in terms of the availability of food within the nesting territory. However, the time and energy expenditure for food gathering would perhaps be lower for marsh than upland nesting females because the largest food items (odonates) are obtained near the nest site. Also, comparisons between two marshes of different productivity indicate the emergent insects, especially odonates, are an important component of the diet in the dense marsh nesting colonies. Odonates comprised a significantly larger portion of the diet of nestlings in Clarkes Pond than in All Saints Marsh. Both marshes are bordered by deciduous woodlands that are probably equally productive of Lepidoptera, but subjective observations of the abundance of adult odonates indicate All Saints Marsh was less productive of Odonata than Clarkes Pond. This difference in marsh productivity is likely responsible for a larger proportion ($P < 0.01$) of the nests having some mortality due to starvation in All Saints Marsh than in Clarkes Pond (cf. Table 3).

As I indicated earlier the relative abundance of food seems to be similar for nestlings in marshes and uplands, therefore the absolute abundance of food must be much greater in marshes that support much larger and denser nesting colonies than are found in uplands (cf. Table 1). Since clutch size and the number fledged per successful nest is nearly the same in both habitats, while nesting density differs considerably, it would appear that breeding populations may be adjusting their density to suit local conditions of food availability (cf. Brenner, 1966). The occurrence of some starvation in all colonies suggests that no breeding populations were nesting at a density far below the maximum level possible for the available food. On the other hand, it is possible that in a sample of nests from any breeding population, regardless of the relative abundance of food, there will be some starvation due to individual differences in food-getting ability of females. In any case, the relationship between breeding density and food is not simple because complex patterns of social behavior are often the proximate regulators of density and the ultimate factors are difficult to determine (Willson and Orians, 1963). Obvious differences in the phenology of vegetation used as nest support are also correlated with differences in nesting density. However, the absolute abundance of food is likely another ultimate factor in the determination of nesting density as regulated by territory size.

SUMMARY

Growth rates of Red-winged Blackbird nestlings in marsh and upland habitats are similar in that they result in the same mean weight at fledging.

The percentage of nests with some nestlings starving, and the percentage of nestlings that die from starvation are similar in both habitats. The mean number fledged per successful nest is also similar between habitats. There is, however, in both habitats, a trend of increasing nestling starvation as the season progresses.

It is suggested that the relative abundance of food is approximately the same for nestlings in either marshes or uplands, but that a higher absolute abundance of food in marshes makes large, dense nesting colonies possible. The relationship between nesting density and food supply is not simple because obvious differences in the phenology of vegetation used as nest support are also correlated with colony size and density.

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NEW LIFE MEMBER

A recent addition to the Life Members of The Wilson Ornithological Society is Edward J. Danforth of Orono, Maine. Mr. Danforth has retired from a job with the New York Telephone Company, and now spends his time in a variety of activities involving ornithology and outdoor recreation. His interests extend to nature photography, and lectures on nature. He writes a weekly column on nature for a local newspaper, and is currently writing a book on nature. He holds a degree from Rutgers University, and is a member of the A.O.U. Mrs. Danforth is also interested in nature, and the Danforths have two children and one grandchild. Our picture shows him exhibiting a sapsucker hole to a group of school children, another of his variety of activities.